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Succession and management of tropical dry forests in the Americas: Review and new perspectives

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ABSTRACT

Understanding tropical forest succession is critical for the development of tropical forest conservation strategies worldwide, given that tropical secondary forests can be considered the forests of the future. Tropical dry forests (TDF) are among the most threatened tropical ecosystems, there are more secondary forests and forest restoration efforts that require a better understanding of successional processes. The main goal of this synthesis for this special issue on the ecology and management of tropical dry forests in the Americas is to present a summarized review of the current knowledge of the ecology and management implications associated to TDF succession. We explore specific issues associated to tropical dry forest succession with emphasis on the use of chronosequences, plant diversity and composition, plant phenology and remote sensing, pollination, and animal–plant interactions; all under the integrating umbrella of ecosystem succession. We also emphasize the need to conduct socio-ecological research to understand changes in land-use history and its effects on succession and forest regeneration of TDF. We close this paper with some thoughts and ideas associated with the strong need for an integrating dimension not considered until today: the role of cyberinfrastructure and eco-informatics as a tool to support sound conservation, management and understanding of TDF in the Americas.

1. Introduction

Understanding tropical forest succession is critical for the development of tropical forest conservation strategies worldwide, given that tropical secondary forests can be considered the forests of the future (Wright, 2005; Sanchez-Azofeifa et al., 2005). Past and present rates of tropical land conversion clearly indicate that most mature tropical forests will eventually disappear leaving behind a complex landscape consisting of a matrix of agricultural fields and forest patches under different levels of succession. This is particularly the case of tropical dry forests (TDF) that remain currently exposed to several threats resulting from human activity (Sanchez-Azofeifa et al., 2005; Miles et al., 2006). Understanding tropical succession in the context of different ecological and human dimensions represents one of the key present challenges to promote and develop conservation and management programs for this threatened ecosystem.

The land cover matrix in the tropics is composed of an astonishing diversity of life forms and species that have been shaped by natural selection and biotic and abiotic factors associated with a wide variety of different habitats. Tropical rainforests are just one of them, but our fascination with their extent and high number of species have driven the forces that contribute to our understanding of tropical ecology. We claim that

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many other vegetation formations, some of large extension such as savannas and dry forests, constitute other regions of major biological importance but are much less understood.

Approximately 42% of tropical forests around the world are TDF (Murphy and Lugo, 1986; Miles et al., 2006), although most knowledge in tropical forest succession has been obtained from rain forest plant communities (Vieira and Scariot, 2006). A search on the ISI Web of Science database from 1900 until March 2009 for articles with the words "succession", and "tropic*" in the title and summary, indicate a great difference in the number of studies conducted in each ecosystem (436 in "rain forest" vs. 60 papers in "dry forest"). In addition, TDF have been extensively transformed and occupied by urban and agricultural areas at significantly higher rates than tropical rainforests (Murphy and Lugo, 1986). For example, just in Latin America alone, approximately 66% of TDF have already been destroyed (Portillo, personal communication). Hence, we must better understand the ecology of succession and the effects of forest management programs on these other equally important ecosystem around the world.

A review of dry tropical forest ecology originally predicted that this ecosystem was likely to recover more quickly to a mature state than do wet forests because of the relative simplicity and small structure of mature forests, and the predominance of coppicing after disturbance (Ewel, 1977; Murphy and Lugo, 1986; Segura et al., 2003). However, these interpretations have been based on speculations with very little empirical evidence. If succession is a slower process in tropical dry than rainforests, in terms of plant growth and other developmental features (Ewel, 1977; Murphy and Lugo, 1986), it is contradictory to expect faster rates of succession for TDF. Apparently, coppicing from stumps and roots remaining after disturbance is expected to take less time to reach maturity and it is considered as the primary regeneration mechanism of disturbed tropical dry sites (Ewel, 1977; Murphy and Lugo, 1986). However, a review of plant sexual expression and mating systems of TDF indicates that the predominant mode of reproduction is through a wide variety of sexual systems where seeds are mainly produced via outcrossing (Quesada et al., in press). Under clonal asexual reproduction (as suggested through coppicing) we should expect low genetic variation in tree populations; however, evidence shows high genetic diversity among adult tree populations that can only be attributable to sexual reproduction via seed dispersal and seedling regeneration (Hamrick and Loveless, 1986; James et al., 1998; Quesada et al., 2004, in press).

Janzen (1988) stated that restoration of dry forest pastures might follow two different patterns, occurring at the same time: one controlled by wind-dispersed tree seeds and another controlled by seeds defecated by animals. Therefore, it is unlikely that ecological succession of TDF is a process that reaches a mature state relatively fast as suggested above by several authors. In fact, it has been proposed that TDF should be even more susceptible to human disturbance because growth rate and regeneration of plants is slow, reproduction is highly seasonal and most plants are mainly outcrossed and dependent on animal pollination (Bawa, 1974, 1990; Frankie et al., 1974; Murphy and Lugo, 1986; Hamrick and Murawski, 1990; Bullock, 1995; Jaimes and Ramirez, 1999; Quesada et al., 2001, 2004, in press; Cascante et al., 2002; Fuchs et al., 2003).

More recently, it has been proposed that seasonality and gap dynamics are the main drivers of regeneration dynamics in TDF, affecting forest composition and structure (Quigley and Platt, 2003). Seasonality as an integral aspect of TDF is well known to affect phenological processes that control vegetative growth and plant reproduction, thereby controlling the regeneration of these forests (Frankie et al., 1974; Opler et al., 1980). However, the importance of gap dynamics has been suggested for tropical rainforests but remain to be tested in TDF where light dynamics and water availability change annually and tree mortality usually occurs with dead standing stems. Therefore, the main mechanisms of succession and regeneration of TDF still remain unexplored and more efforts are required to understand ecological processes of these important ecosystems.

The main goal of this synthesis for this special issue on the ecology and management of TDF in the Americas is to present a summarized review of the current knowledge of the ecology and management implications associated to TDF succession. We explore specific issues associated to ecological succession with emphasis on the use of chronosequences, plant diversity and composition, plant phenology and remote sensing, pollination, and animal–plant interactions, all under the integrating umbrella of ecosystem succession. We also emphasize the need to conduct socio-ecological research to understand changes in land-use history and its effects on succession and forest regeneration of TDF. We close this paper with some thoughts and ideas associated with the strong need for an integrating dimension not considered until today: the role of cyberinfrastructure and eco-informatics as a tool to support sound conservation, management and understanding of TDF in the Americas.

2. Ecological succession

2.1. The role of chronosequence work applied to TDF

In general, different approaches have been proposed to study succession: long-term study, stratigraphy, palynology, stand reconstruction and chronosequences (Johnson and Miyanishi, 2008). Among these approaches the chronosequence has been one of the most used methods (Chazdon et al., 2007). This method uses multiple sites of different ages to examine successional changes of plant species composition in communities (Lehmkuhl et al., 2003; Kalacska et al., 2005). Chronosequence studies have provided extensive information on successional patterns of tropical forests in a variety of life-zones, soil types, and land-use categories (Aplet and Vitousek, 1994; Zimmerman et al., 1995; Aide et al., 2000; Pascarella et al., 2000; Rivera et al., 2000; Kennard, 2002; Kalacska et al., 2005; Madeira et al., 2009). These studies have emphasized the importance of age since abandonment and land-use history on forest structure and species composition (Aide et al., 1996; Pascarella et al., 2000; González-Iturbe et al., 2002; Kalacska et al., 2005; Madeira et al., 2009). However, strong criticism has been formulated about the use of chronosequences. This criticism is centered on the fact that the main assumption associated to chronosequence research, that each site on a given chronosequence has the same history of both abiotic and biotic components, is difficult to prove. This former assumption is almost impossible to achieve, particularly in the tropics where there is a high degree of spatial heterogeneity. Indeed, most chronosequence studies justify their use by considering sites with similar soil type, topographic position and/or land-use history (Pascarella et al., 2004; Bischoff et al., 2005; van Breugel et al., 2007; Lebrija-Trejos et al., 2008; Vargas et al., 2008).

Some long-term studies, concerned about the limitations on approaches applying chronosequences have been conducted to determine whether changes that actually occur over time within sites do in fact represent different successional stages (Sheil et al., 2000; Sheil, 2001; Pascarella et al., 2004; Chazdon et al., 2007). Trends in attributes such as basal area have been adequately predicted from chronosequences (Chazdon et al., 2007; Pascarella et al., 2004) whereas differences are found with respect to species richness/density (Sheil, 2001; Pascarella et al., 2004; Chazdon et al., 2007) and species composition (Chazdon et al., 2007; Johnson and Miyanishi, 2008).